THE RAFFLES BULLETIN OF ZOOLOGY 2007 **55**(2): 389–395
Date of Publication: 31 Aug.2007

POPULATION DYNAMICS OF ARBOREAL AND TERRESTRIAL SMALL MAMMALS IN A TROPICAL RAINFOREST, SARAWAK, MALAYSIA

Michiko Nakagawa
Research Institute for Humanity and Nature, Kamigamo, Kyoto 603-8047, Japan.
Present address: Laboratory of Forest Ecology and Physiology, Graduate School of Bioagricultural Sciences, Nagoya University, Nagoya 464-8601, Japan.
Email: miko@agr.nagoya-u.ac.jp (Corresponding author)

Hideo Miguchi
Department of Production and Environmental Sciences, Faculty of Agriculture, Niigata University, Igarashi, Niigata 950-2181, Japan
Email: mig-chi@agr.niigata-u.ac.jp

Kaori Sato
Japan Wildlife Research Center, Tokyo, Japan
Email: ksato@jwrc.or.jp

Shoko Sakai
Center for Ecological Research, Kyoto University, Kamitanakami-Hirano, Otsu 520-2113, Japan
Email: shoko@ecology.kyoto-u.ac.jp

Tohru Nakashizuka
Present address: Graduate School of Life Sciences, Tohoku University, Sendai 980-8578, Japan.
Email: toron@mail.tains.tohoku.ac.jp

ABSTRACT. – Lowland tropical forests of Southeast Asia are characterized by general flowering, i.e. irregular and supra-annual fluctuations in flower and fruit production at the community level. We examined the relationship between general flowering and the population dynamics of arboreal and terrestrial small mammals using live-trapping data obtained over 9 years in a lowland tropical forest, Sarawak, Malaysia. The abundance of arboreal and terrestrial small mammals, immature *Maxomys rajah* (the most commonly caught terrestrial rat) and adult *Callosciurus prevostii* (a relatively large species and the most commonly caught arboreal squirrel) were significantly negatively correlated with the percentage of fruiting trees with and/or without a one- to two-month lag. The abundance of terrestrial small mammals and immature *M. rajah* were significantly positively correlated with the percentage of fruiting trees six and five months earlier, respectively. These results indicate that a time lag occurred between fruit production and increases in small mammal populations. Differences in the age classes between the two most commonly caught species during population growth suggest that population increases associated with general flowering were caused by both the recruitment of young individuals of small mammals with relatively low dispersal ability (*M. rajah*) and the immigration of adult individuals with high dispersal ability (*C. prevostii*).

KEY WORDS. – General flowering, immigrant, recruitment, rodent, treeshrew.

INTRODUCTION

Small mammal population dynamics have been of great interest to ecologists and numerous studies have been conducted on various species and regions (Saitoh, 1987; Fryxell et al., 1998; Tkadlec & Stenseth, 2001; Jaksic & Lima, 2003). Food availability or quality is one of the most important factors that affect population fluctuations of small mammals (Selås, 1997). Densities of rodents in the spring or summer increase after acorn mast-fruiting, because stored acorns are important food for rodents during the winter (Wolff, 1996; Abe et al., 2005). The chemical composition of food plants also affects the population of bank voles through increased winter survival (Selås et al., 2002). However, these reports are mostly from temperate or northern European regions, and information on the long-term population dynamics of small mammals in tropical regions is extremely scarce. Wood (1984) and Langham (1982) reported on 10-year and two-year studies of the population dynamics of tropical rodents in an oil palm plantation and a primary forest in Malaysia, respectively, although no information on food availability or quality was provided. Lee (1997) found a relationship between population abundances of rodents and crop loss in a cocoa plantation but not in a natural forest. In addition, most studies have investigated small terrestrial mammals because of difficulties in accessing treetops to investigate the canopy; thus, the population dynamics of arboreal small mammals have rarely been documented (Klenner & Krebs, 1991; Kays & Allison, 2001). Moreover, research on arboreal small mammals in tropical regions only began in the last decade and even general information about the fauna is still limited (Malcolm, 1991, 1995; Akbar & Ariffin, 1997; Wells et al., 2004, 2006).

The lowland tropical forests of Southeast Asia are characterized by general flowering (GF), i.e. irregular and supra-annual fluctuations in flower and fruit production at the community level (Ashton et al., 1988; Appanah, 1993; Sakai et al., 1999; Sakai 2002). During GF periods, most dipterocarps and trees of many other families bloom consecutively or simultaneously for several months at both the population and community level. They then produce numerous fruits or seeds synchronously after flowering (Sakai, 2002), creating an abrupt supply of massive food resources. Various fruits are eaten by small mammals in Southeast Asian forests (Blate et al., 1998; Curran & Webb, 2000; Kitamura et al., 2006). Thus, small mammal populations may fluctuate in response to GF because food availability has long been recognized as a major factor affecting animal population dynamics (Dobson & Kjelgaard, 1985; Wolff, 1996; Gentile et al., 2004). Because the fruits of dipterocarp trees (which are dominant in lowland tropical forests of Asia) are high-quality food for mammals, local anecdotal evidence indicate increases in some populations of mammals (e.g., wild boar). However, there is little current scientific data regarding the relationship between mammal population dynamics and GF (Curran & Leighton, 2000). Adler (1998), based on food-supplementation experiments, reported that increases in rodent population were due to increased production and recruitment of young individuals, rather than heightened immigration or survival of adults. This result likely applies to rodents with low dispersal ability, whereas those with high dispersal ability, such as large squirrels, may disperse from other areas to those of plentiful resources. The home ranges of squirrels in Malaysia cover more than 3.5 ha, while those of smaller tropical rats sometimes cover only 0.2 ha (Saiful et al., 2001; Nakagawa, pers. obs.).

We examined nine years of live-trapping records for arboreal and terrestrial small mammals in a lowland tropical forest in Borneo to determine the relationship between sporadic community-level tree fruiting (GF) and small-mammal population dynamics. To evaluate the possible mechanisms underlying the increase in small mammal abundance, we also analyzed the population dynamics of different age classes (based on body weight) of the most commonly caught arboreal and terrestrial species. If the immigration of adult individuals from neighboring areas contributes to the population increase, the abundance of adult individuals would be significantly correlated with fruiting intensity. If reproduction and recruitment of young individuals within the area contributes to the population increase, the abundance of immature individuals would be significantly correlated with fruiting intensity. Because of the difficulty in identifying the age classes of rodents, we used body weight as an indicator of age class. Our goals were to determine whether significant correlations exist between the abundance of small mammals (both arboreal and terrestrial) and fruiting intensity, as well as to identify the age classes (i.e. immature or adult) contributing most to the population increase.

MATERIALS AND METHODS

Study site and phenology observations

The study took place at Lambir Hills National Park, Sarawak, Malaysia (4°2'N 113°5'E; 150 m a.s.l.). Most of the park is covered by primary lowland forest dominated by dipterocarp trees in the emergent and canopy layers and species of Euphorbiaceae, Burseraceae and Myristicaceae in the lower layers (Lafrankie et al., 1995). The climate is perhumid, with a mean annual precipitation of nearly 2,700 mm and monthly precipitation seldom < 100 mm. The flowering and fruiting phenology of various trees has been monitored at the site since 1992 (Sakai et al., 1999). As an indicator of community-level fruiting intensity, we calculated the percentage of fruiting trees that were observed during the phenology monitoring. See Sakai et al. (1999) for details of the phenology census. In November 2000, we also set sixty-five 0.5 m^2 seed traps in a 20 m grid to monitor fluctuations in fallen fruits. The seed traps were made of 1 mm nylon mesh and were placed 1 m above the ground. Fruits were collected from the seed traps once or twice each month, oven-dried for 48 hours at 50°C, and weighed to the nearest 1 mg.

Small-mammal trapping

Small mammals were live-trapped from August 1997 to December 2005 (100 months), except in 2000 (Table 1). To trap terrestrial small mammals, 48 wire-mesh live traps were placed on the ground in a 20 m grid (covering 60 × 220 m). We also placed 25 live traps above the ground, including in the subcanopy and canopy layers (3–45 m in height) of 4 emergent dipterocarp trees that were located within the ground-trapping area. The distribution of above-ground traps were three traps at 3–10 m, three at 10–20 m, five at 20–30 m, six at 30–40 m, and eight at 40–45 m. To access the above-ground traps, we used a canopy observation system (tree towers, ladders, and walkway) that was established in 1992 (Inoue & Hamid, 1994; Inoue et al., 1995). Each live trap was 15 × 12 × 30 cm, baited with banana and sweet potato, and covered with a sheet of transparent plastic to exclude rain. Traps were set for three to five consecutive nights one to four times each year (Table 1). The total effective arboreal and terrestrial trapnights were 1,883 and 3,473, respectively. We checked all live traps once a day

Table 1. The months that small mammal trappings were conducted. Numbers of census nights and effective trapnights are also shown.

Year	Month	Census nights	Terrestrial effective trapnights	Arboreal effective trapnights
1997	August	3[a]	60	80
	December	4	178	95
1998	January	4	175	106
	March	4	167	92
	August	5	225	111
	September	5	225	111
1999	March	3	125	56
	July	5	231	90
2001	May	3	131	67
	September	5	156	109
2002	January	3	142	72
	March	3	92	61
2003	September	5	240	125
2004	April	5	217	120
	July	5	223	123
	November	5	187	117
2005	March	5	236	105
	July	5	235	122
	December	5	228	121
Total			3473	1883

[a]For arboreal trapping, census night was four nights

during the morning (0700 – 1100 hours), and all captured small mammals were toe-clipped for permanent individual identification. After marking and recording their species, sex, weight and capture point, individuals were immediately released at the site of capture. Species identification and nomenclature follow that of Payne et al. (2005).

Data analysis

The population of small mammals at each trapping period was calculated as the number of arboreal or terrestrial animals captured per 100 trapnights. Mammals that were captured ≥ 20 m above the ground and those captured ≤ 3 m and on the ground were classified as exclusively arboreal and terrestrial, respectively. For species captured above and on the ground, we classified them into scansorial small mammals. In this paper, we refer to scansorial and exclusively arboreal species as arboreal small mammals. Correlations between the abundance of arboreal or terrestrial small mammals and the percentages of fruiting trees in the same month and 1–6 months earlier were evaluated using Pearson's correlation tests. Because of the likelihood of a time lag between an increase in fruit abundance and an increase in small mammal abundance, we assessed these correlations to the fruiting of trees up to 6 months earlier. Considering the observed range of body weight, the most commonly caught terrestrial and arboreal small mammals were classified into two age classes by body weight: immature, less than the mean weight; and adult, more than the mean weight. To explore the mechanisms of population increase, we evaluated the correlation between the abundance of each age class and the percentages of fruiting trees in the same month and 1–6 months earlier using Pearson's correlation tests. All statistical analyses were performed using JMP 4.0 (SAS Institute, 2000).

RESULTS

Arboreal and terrestrial small-mammal communities

In total, we captured 369 individuals of 19 species, including treeshrews, squirrels, rats, and a slow loris (Table 2). Of these, four species were trapped only above 20 m from the ground (exclusively arboreal), nine species were trapped on the ground and no more than 3 m from the ground (terrestrial), and six species were recorded both on and above the ground (scansorial). The brown spiny rat (*Maxomys rajah*) was the most commonly caught terrestrial small mammal, followed by whitehead's rat (*M. whiteheadi*) and the large treeshrew (*Tupaia tana*). Prevost's squirrel (*Callosciurus prevostii*) was the most commonly caught arboreal mammal, although it was occasionally observed on the ground and had scansorial habitat use.

Table 2. Small mammals captured at Lambir Hills National Park from August 1997 to December 2005. Habitat usage and average weight and weight range (in g) are also shown.

Species	Common name	Habitat use	N	Ave. weight (range) (g)
SCANDENTIA				
Tupaiidae				
Ptilocercus lowii	Pentail treeshrew	Scansorial	5	54.5 (34-66)
Tupaia minor	Lesser treeshrew	Scansorial	4	59.0 (51-64)
Tupaia splendidula	Ruddy treeshrew	Terrestrial	7	184.1 (150-220)
Tupaia glis	Common treeshrew	Terrestrial	6	220.5 (175-279)
Tupaia tana	Large treeshrew	Terrestrial	24	256.1 (175-305)
RODENTIA				
Sciuridae				
Petinomys vordermanni	Vordermann's flying squirrel	Exclusively arboreal	3	48.0 (47-50)
Sundasciurus lowi	Low's squirrel	Terrestrial	11	109.5 (86-135)
Callosciurus notatus	Plantain squirrel	Scansorial	4	235.5 (235-236)
Callosciurus prevostii	Prevost's squirrel	Scansorial	48	391.6 (230-480)
Muridae				
Chiropodomys gliroides	Common pencil-tailed tree-mouse	Exclusively arboreal	12	15.8 (10-29)
Chiropodomys major	Large pencil-tailed tree-mouse	Exclusively arboreal	10	36.9 (19-51)
Maxomys whiteheadi	Whitehead's rat	Terrestrial	59	47.7 (30-80)
Maxomys rajah	Brown spiny rat	Terrestrial	127	145.8 (66-360)
Rattus exulans	Polynesian rat	Terrestrial	2	49.0 (45-53)
Niviventer cremoriventer	Dark-tailed tree rat	Terrestrial	22	69.0 (32-84)
Lenothrix canus	Grey tree rat	Scansorial	1	210.0210
Sundamys muelleri	Muller's rat	Scansorial	18	262.5 (165-382)
Leopoldamys sabanus	Long-tailed giant rat	Terrestrial	4	325.3 (291-375)
PRIMATES				
Lorisidae				
Nycticebus coucang	Slow loris	Exclusively arboreal	2	595.0 (556-640)

[a]Terrestrial: Few or no records above 3 m. Scansorial: small mammals that were captured both above and on the ground. Exclusively arboreal: few or no records below 20 m.

Population dynamics associated with GF

General flowering and consecutive fruiting occurred five times during the study period: 1997, 1998, 2001, 2004 and 2005 (Fig. 1a). The percentage of trees that produced fruits in 2001 and 2005 was higher than that in 1997, 1998, and 2004. Although the fluctuating pattern of fruit production from phenology observations was consistent with that of seed traps, the peak of fruit occurrence in seed traps was several months later than that in the phenology census because of a time lag in fruit-fall.

Populations of both arboreal and terrestrial small mammals fluctuated considerably corresponding to GF, and their patterns were approximately similar (Fig. 1b). Significant negative correlations were detected between the abundance of arboreal small mammals and proportion of fruiting trees in the same ($r = -0.594$, $P < 0.01$) and previous ($r = -0.531$, $P < 0.05$) months (Table 3). The abundance of terrestrial small mammals was significantly negatively-correlated with the proportion of fruiting trees in the same month ($r = -0.503$, $P < 0.05$), and positively-correlated with the proportion of fruiting trees 6 months earlier ($r = 0.473$, $P < 0.05$).

In the case of the most commonly caught terrestrial *M. rajah*, immature individuals were observed mostly during population increases (Fig. 1c). Significant negative correlations were detected between the number of immature *M. rajah* and the proportion of fruiting trees in the same month ($r = -0.56$, $P < 0.05$; Table 3). Significant positive correlations were observed between the number of immature *M. rajah* and the proportion of fruiting trees 5 months earlier ($r = 0.478$, $P < 0.05$). In contrast, significant negative correlations existed between the number of adult *C. prevostii* and the proportion of fruiting trees in the same month and 1–2 months earlier.

Table 3. Correlations between the abundance of small mammals and the percentage of fruiting individual trees with lags of zero to six months. Only significant results are shown.

Abundances of small mammals	Percentage of fruiting trees[a]				
	Present month	Previous month	Two months earlier	Five months earlier	Six months earlier
Arboreal small mammals	-0.594**	-0.531*			
Terrestrial small mammals	-0.503*				0.473*
Immature *Maxomys rajah*	-0.560*			0.478*	
Adult *Callosciurus prevostii*	-0.636**	-0.618**	-0.548*		

[a]; *$P < 0.05$, **$P < 0.01$

DISCUSSION

Arboreal and terrestrial small-mammal assemblage composition at Lambir Hills

The major arboreal and terrestrial small mammals at Lambir Hills National Park were approximately similar to those in other dipterocarp forests in Asia (Nor, 2001; Wells et al., 2004; Kitamura et al., 2006; Suzuki et al., 2007). Amongst the 19 species captured, the ruddy treeshrew (*Tupaia splendidula*) and the large pencil-tailed tree-mouse (*Chiropodomys major*) are endemic to Borneo. Vordermann's flying squirrel (*Petinomys vordermanni*) has never been recorded in Sarawak (Payne et al., 2005), possibly in part because its habitat is restricted to subcanopy and canopy layers and its small body size is easy to overlook. This clearly indicates the importance of gathering further information about arboreal small mammals using live traps in tropical regions.

Figure 1

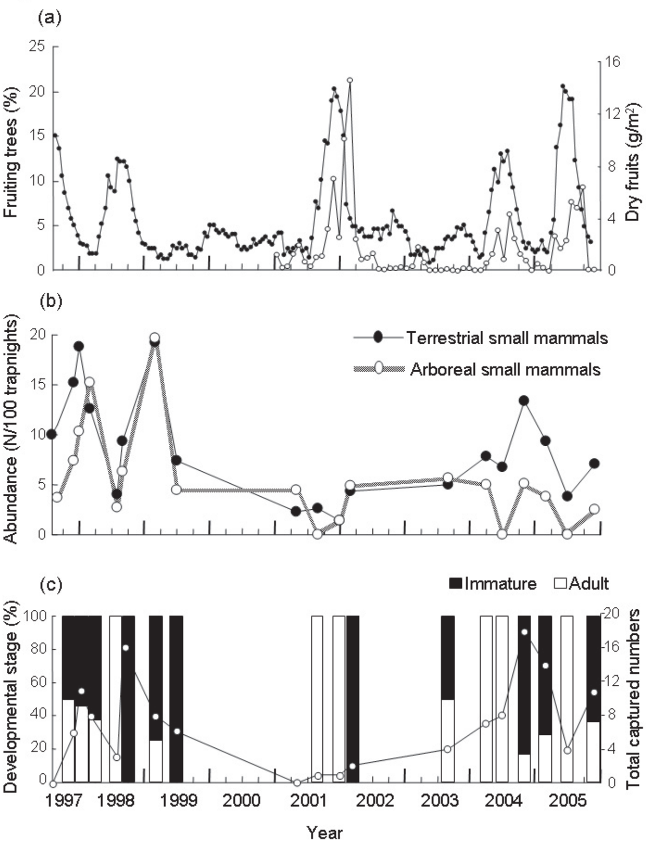

Fig. 1. Temporal patterns at Lambir Hills National Park, Sarawak, Malaysia, from August 1997 to December 2005. (a) percentage of fruiting trees obtained by phenology observation (%; black circle), together with weight of dried fruits obtained by seed traps from November 2000 to December 2005 (g/m^2; white circle); (b) population dynamics per 100 trapnights of arboreal and terrestrial small mammals; (c) percentage of the two age classes (immature and adult) of *Maxomys rajah*. Total numbers of captured *M. rajah* at each census were shown.

All treeshrews and flying squirrels are protected animals and slow loris is totally protected in Sarawak (Wildlife Protection Ordinance, 1998). Observations of several species of treeshrews and one species of flying squirrel and slow loris in the study site indicates that the primary forest of the National Park may be crucial habitat for protected animals, including various small mammals. Proper management of the park is important to conserve mammal diversity in this region.

Relationship between small-mammal population dynamics and GF

The response of arboreal and terrestrial small mammals to GF was similar, and small-mammal populations fluctuated according to GF. Because of the time lag in the food supply for arboreal and terrestrial small mammals (i.e. the latter can eat only fallen fruits), the population increase in the former would be expected to precede that of the latter. However, we did not detect such a pattern. This may reflect the fact that species that are mostly active on the ground also sometimes climb trees, and many arboreal species occasionally found on the ground and had scansorial habitat uses. Similar observations about habitat use have been reported at other study sites in tropical forests (Lim, 1970; Wells et al., 2006), and the dichotomy between terrestrial and arboreal small mammals may merely being a simplified classification of the vertical gradients in habitat use.

Significant negative correlations between small-mammal abundance and fruiting intensity in the same month and/or one month earlier indicate that the abundance of small mammals was low when trees were fruiting, increased after the fall of mature fruits, and then decreased quickly. Because small-mammal populations were lowest during the peak of fruiting, which occurred in two consecutive years, predator satiation may have occurred, with more fruit escaping predation. Curran & Leighton (2000) reported higher predation avoidance of dipterocarp fruits from nomadic mammals (wild boars). Our results suggest the possibility of escaping fruit predation from resident small mammals. The significant positive correlation indicates that small-mammal populations peaked 6 month after the peak of fruiting. However, because of a time lag of several months between the peak of fruiting, as observed both phenologically and in seed traps, populations of terrestrial small mammals, which feed on the forest floor, peaked 3-4 months after fruit-fall. Many fruits in the study site (including dipterocarp fruits) have no dormancy and germinate soon after fruit fall, with seedlings becoming established 3–4 months after fruit-fall (Itoh, 1995; Curran & Webb, 2000). A time lag of several months may contribute to the success of seedling establishment by avoiding the high pressure of fruit predation.

The abundance of small mammals increased two to three times that of low-density periods (non-GF periods) in every GF year. In contrast, the scale of GF, i.e. the percentage of fruiting individuals, varied among GF years, indicating a higher possibility of preventing fruit predation in greater GF years. The relationship between the scale of GF and small-mammal population increases is an interesting theme with regard to aspects of tree regeneration through predator satiation, although more data are required to examine this relationship. Flowers and fruits of figs are available in small amounts throughout the year, independent of GF, and many animals eat figs (Harrison et al., 2000; Shanahan et al., 2001). During the non-GF period, small mammals may survive by eating figs, new leaves and shoots as well as insects.

The mechanism of the small-mammal population increase associated with GF appears to differ among species. In the case of *M. rajah*, immature individuals were significantly correlated with fruiting intensity and were observed mostly during the phase of population increase, suggesting that *M. rajah* breed during GF. Resource supplementation results in increases in juvenile recruitment or numbers of births per adult female (Klenner & Krebs, 1991; Adler, 1998). Gurnell (1996) also reported that female reproductive success was positively-correlated with food availability. Not only the amount of food but also its quality affects female reproductive success; for example, acorns that are high in lipids and carbohydrates are necessary for black bears to withstand winter denning, reproduction, and lactation (Clark, 2004). Fruits of dipterocarps are nutritious and contain high concentrations of lipids and carbohydrates (Nakagawa & Nakashizuka, 2004). High-energy food sources such as dipterocarp fruits may be crucial for the successful reproduction of small mammals. Although little is known of the life history and ecology of *M. rajah* (Harrison, 1955), given that the time lag between the peak in fallen fruits and that in the terrestrial small-mammal populations was 3–4 months, the reproductive activities of *M. rajah*, including pregnancy and nursing, may require 3–4 months. In contrast, the abundance of adult *C. prevostii* increased after the peak of fruiting, indicating that the immigrant of adult individuals may contribute to the population increases associated with GF. The home ranges of *Callosciurus* squirrels range from 0.7–2.3 ha (Saiful et al., 2001) and small mammals that are highly mobile, such as *C. prevostii*, may seek areas where fruits are abundant. However, given that the increase in the adult population occurs after the peak of fruiting, even though adults feed chiefly in the canopy, immigration and the search for food resources may occur relatively slowly. Further detailed research of population dynamics above and on the ground might improve our understanding about reproduction and dispersal of small mammals.

ACKNOWLEDGMENTS

We are most grateful to L. Chong (Sarawak Forestry Corporation) and J. Kendawang (Forest Department Sarawak) for permission and kind arrangement to conduct research in Sarawak. The field assistances of K. Takahashi, K. Hamamoto, Johan, Jinggan, Ekeh, Umping and Maok have been most helpful. This work was financially supported by RIHN research project 2-2, CREST program of the Japan Science and Technology Corporation, the Ministry of Education, Science, Sports, and Culture, Grant-in-Aid for Scientific Research 16405006, and JSPS Research Fellowships for Young Scientists to M. N.

LITERATURE CITED

Abe, M., H. Miguchi, A. Honda, A. Makita & T. Nakashizuka, 2005. Short-term changes affecting regeneration of *Fagus crenata* after the simultaneous death of *Sasa kurilensis*. *Journal of Vegetation Science,* **16:** 49–56.

Adler, G. H, 1998. Impacts of resource abundance on populations of a tropical forest rodent. *Ecology,* **79:** 242–254.

Akbar, Z. & M. K. E. Ariffin, 1997. A comparison of small mammal abundance between a primary and disturbed lowland rain forest in Peninsular Malaysia. *Malayan Nature Journal,* **50:** 201–206.

Appanah, S., 1993. Mass flowering of dipterocarp forests in the aseasonal tropics. *Journal of Bioscience,* **18:** 457–474.

Ashton, P. S., T. J.Givnish & S. Appanah, 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *American Naturalist,* **132:** 44–66.

Blate, G. M., D. R. Peart & M. Leighton, 1998. Post-dispersal predation on isolated seeds: a comparative study of 40 tree species in a Southeast Asian forest. *Oikos,* **82:** 522–538.

Clark, J. D., 2004. Oak-black bear relationships in Southeastern uplands. *General Technical Report,* **SRS-73:** 116–119.

Curran, L. M. & M. Leighton, 2000. Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecological Monograph,* **70:** 101–128.

Curran, L. M. & C.O. Webb, 2000. Experimental tests of the spatiotemporal scale of seed predation in mast-fruiting Dipterocarpaceae. *Ecological Monograph,* **70:**129–148.

Dobson, F. S. & J. D. Kjelgaard, 1985. The influence of food resources on population dynamics in Columbian ground squirrels. *Canadian Journal of Zoology,* **63:** 2095–2104.

Fryxell, J. M., J. B. Falls, E. A. Falls & R. J. Brooks, 1998. Long-term dynamics of small-mammal populations in Ontario. *Ecology,* **79:** 213–225.

Gentile, R., R. Finotti, V. Rademaker & R. Cerqueira, 2004. Population dynamics of four marsupials and its relation to resource production in the Atlantic forest in southeastern Brazil. *Mammalia,* **68:** 109–119.

Gurnell, J., 1996. The effects of food availability and winter weather on the dynamics of a grey squirrel population in southern England. *Journal of Applied Ecology,* **33:** 325–338.

Harrison, J. L., 1955. Data on the reproduction of some Malayan mammals. *Proceeding of the Zoological Society London,* **125:** 445–460.

Harrison, R. D., N. Yamamura & T. Inoue, 2000. Phenology of a common roadside fig in Sarawak. *Ecological Research,* **15:** 47–61.

Inoue, T. & A.a. Hamid, 1994. *Plant reproductive system and animal seasonal dynamics: long-term study of dipterocarp forests in Sarawak*. Center for Ecological Research, Kyoto University, Kyoto, Japan.

Inoue, T., T. Yumoto, A. A. Hamid, H. S. Lee & K. Ogino, 1995. Construction of a canopy observation system in a tropical rainforest of Sarawak. *Selbyana,* **16:** 100–111.

Itoh, A., 1995. Effects of forest floor environment on germination and seedling establishment of two Bornean rainforest emergent species. *Journal of Tropical Ecology,* **11:** 517–527.

Jaksic, F. M. & M. Lima, 2003. Myths and facts on ratads: bamboo blooms, rainfall peaks and rodent outbreaks in South America. *Austral Ecology,* **28:** 237–251.

Kays, R. & A. Allison, 2001. Arboreal tropical forest vertebrates: current knowledge and research trends. *Plant Ecology,* **153:** 109–120.

Kitamura, S., S. Suzuki, T. Yumoto, P. Poonswad, P. Chuailua,K. Plongmai, T. Maruhashi, N. Noma & C. Suckasam, 2006. Dispersal of *Canarium euphyllum* (Burseraceae), a large-seeded tree species, in a moist evergreen forest in Thailand. *Journal of Tropical Ecology*, **22:** 137–146.

Klenner, W. & C. J. Krebs, 1991. Red squirrel population dynamics. I. The effect of supplemental food on demography. *Journal of Animal Ecology,* **60:** 961–978.

LaFrankie, J. V., S. Tan & P. S. Ashton, 1995. *Species list for the 52-ha forest dynamics research plot Lambir Hills National Park, Sarawak, Malaysia*. Center of Tropical Forest Science, Internal Report, Boston.

Langham, N. P. E., 1982. The ecology of the tree shrew, *Tupaia glis* in Peninsular Malaysia. *Journal of Zoology (Lond.)*, **197:** 323–344.

Lee, C. H., 1997. Field rodent population abundance and cocoa crop loss. *Journal of Tropical Agriculture and Food Science,* **25:** 25–41.

Lim, B. L., 1970. Distribution, relative abundance, food habits, and parasite patterns of giant rats (*Rattus*) in west Malaysia. *Journal of Mammalogy,* **51:** 730–740.

Malcolm, J. R., 1991. Comparative abundances of Neotropical small mammals by trap height. *Journal of Mammalogy,* **72:** 188–192.

Malcolm, J. R., 1995. Forest structure and the abundance and diversity of Neotropical small mammals. In: Lowman, M. D. & M. N. Nadkarni (eds.), *Forest Canopies*. Academic Press. Pp. 179–197.

Nakagawa, M. & T. Nakashizuka, 2004. Relationships between physical and chemical characteristics of dipterocarp seeds. *Seed Science Research,* **14:** 363–369.

Nor, S. M. D., 2001. Elevational diversity patterns of small mammals on Mount Kinabalu, Sabah, Malaysia. *Global Ecology and Biogeography,* **10:** 41–62.

Payne, J., C. M. Francis & K. Phillipps, 2005. *A field guide to the Mammals of Borneo*. The Sabah Society, Kota Kinabalu.

Saiful, A. A., A. H. Idris, Y. N. Rashid, N. Tamura & F. Hayashi, 2001. Home range size of sympatric squirrel species inhabiting a lowland dipterocarp forest in Malaysia. *Biotropica,* **33:** 346–351.

Saitoh, T., 1987. A time series and geographical analysis of population dynamics of the red-backed vole in Hokkaido. *Oecologia,* **73:** 382–388.

Sakai, S., 2002. General flowering in lowland mixed dipterocarp forests of South-east Asia. *Biological Journal of the Linnean Society,* **75:** 233–247.

Sakai, S., K. Momose, T. Yumoto, T. Nagamitsu, H. Nagamasu, A.A. Hamid & T. Nakashizuka, 1999. Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. *American Journal of Botany,* **86:** 1414–1436.

SAS Institute, 2000. *JMP user's guide*. SAS Institute, Cary, NC, USA.

Selås, V., 1997. Cyclic population fluctuations of herbivores as an effect of cyclic seed cropping of plants: the mast depression hypothesis. *Oikos,* **80:** 257–268.

Selås, V., E. Framstad & T. K.Spidsø, 2002. Effects of seed masting of bilberry, oak and spruce on sympatric populations of bank vole (*Clethrionomys glareolus*) and wood mouse (*Apodemus sylvaticus*) in southern Norway. *Journal of Zoology (Lond.)*, **258:** 459–468.

Shanahan, M., S. So, S. G.. Compton & R. Corlett, 2001. Fig-eating by vertebrate frugivores: a global review. *Biological Review,* **76:** 529–572.

Suzuki, S., S. Kitamura, M. Kon, P. Poonswad, P. Chuailua, T. Yumoto, N. Noma, T. Maruhashi & P. Wohandee, 2007. Fruit visitation patterns of small mammals on the forest floor in a tropical seasonal forest of Thailand. *Tropics,* **16:** 17–29.

Tkadlec, E. & N. C. Stenseth, 2001. A new geographical gradient in vole population dynamics. *Proceeding of the Royal Society of London Series B,* **268:** 1547–1552.

Wells, K., M. Pfeiffer, M. B. Lakim & K. E. Linsenmair, 2004. Use of arboreal and terrestrial space by a small mammal community in a tropical rain forest in Borneo, Malaysia. *Journal of Biogeography,* **31:** 641–652.

Wells, K., M. Pfeiffer, M. B. Lakim & E. K. V. Kalko, 2006. Movement trajectories and habitat partitioning of small mammals in logged and unlogged rain forests on Borneo. *Journal of Animal Ecology,* **75:** 1212–1223.

Wildlife Protection Ordinance, 1998. *Laws of Sarawak*. Chapter 26. Sarawak Forest Department.

Wolff, J. O., 1996. Population fluctuations of mast-eating rodents are correlated with production of acorns. *Journal of Mammalogy,* **77:** 850–856.

Wood, B. J., 1984. A long-term study of *Rattus tiomanicus* populations in an oil palm plantation in Johore, Malaysia. I. Study methods and population size without control. *Journal of Applied Ecology,* **21:** 445–464.